NOTES ON SOME LITTLE KNOWN AMERICAN FOSSIL TORTOISES.

BY DR. G. BAUR.

1. COMPSEMYS Leidy.

The genus *Compsemys* was established by Prof. Leidy[1] in 1856 on a vertebral and costal bone of a tortoise from the Laramie formation of the Judith River. The only character given at that time, was: "The free surface of all the bones is thickly studded with granular tubercles, which give to it a shagreened appearance, differing from anything observed in recent turtles." The type of the genus is *Compsemys victus* Leidy. It was figured by Prof. Leidy[2] three years later, in the Transactions of the American Philosophical Society. Prof. Cope[3] adopted this genus and referred to it *Emys obscurus* Leidy, published at the same time with *Compsemys victus*. In 1875 he added *Compsemys ogmius* Cope from the Milk River.[4]

In 1876 Prof. Cope[5] established two more species from the Laramie of Montana, under the names of *Compsemys imbricarius*, and *C. variolosus*. All the species described to this date were from the Laramie Formation. In 1877 a new species of *Compsemys* was described by Prof. Cope[6] from the Jurassic Beds of Colorado, under the name of *Compsemys plicatulus*.

The remains of this species were found with those of Dinosaurs by Mr. C. W. Lucas of Canyon City, Colorado; they represent the oldest American tortoise. The species was based on "portions of both carapace and plastron of several individuals."

So far the genus *Compsemys* was only known from the carapace and plastron, from which its characters were taken; "tortoises with

[1] Leidy, Joseph. Notices of extinct Vertebrata discovered by Dr. F. V. Hayden, during the expedition to the Sioux country, under the command of Lieut. G. K. Warren. Proc. Acad. Nat. Sci. Phila., vol. viii, 1856, p. 312, Phila., 1857.

[2] Leidy, Joseph. Extinct Vertebrata from the Judith River and great Lignite Formations of Nebraska. Trans. Am. Philos. Soc. 1859, p. 152, pl. xi., figs. 5, 6, 7.

[3] Cope, E. D. Synopsis of the Extinct Batrachia and Reptilia of North America. Trans. Am. Philos. Soc., vol. xiv, Phila., 1870, p. 124.

[4] Cope, E. D. The Vertebrata of the Cretaceous Formations of the West. Washington, 1875, p. 91.

[5] Cope, E. D. Descriptions of some Vertebrate Remains from the Fort Union Beds of Montana, Paleontol. Bulletin, No. 22, p. 10 (published Nov. 13, 1876), also Proc. Ac. Nat. Sci. Phil., 1876.

[6] Cope, E. D. On Reptilian Remains from the Dakota Beds of Colorado, Paleont. Bulletin, No. 26 (November 21, 1877), pp. 195, 196, reprinted from American Philos. Soc. xvii, 1877, pp, 195, 196.

marginal bones completely united with solid plastron, and the usual dermal scuta, and which differ from *Emys* in their Trionyx-like sculpture." Cope, p. 195.

In 1886, I began my researches on the Testudinata; lately I have examined the collections of the Academy of Natural Sciences of Philadelphia and the Smithsonian Institution, containing the types of Prof. Leidy; also the collection of Prof. Cope who permitted me to study his types at different times with the greatest liberality. The result of my examination is, that *Compsemys* proves to be a member of the Pleurosternidæ, having the pelvis free from carapace and plastron, a complete mesoplastron and a continuous series of neural bones; having also infra-marginals and an intergular. The extensive material of *Compsemys plicatulus* Cope, in the Peabody Museum from the Jurassic of Como, Wyoming, the same locality which yielded the numerous mammals and dinosaurs, was examined at the same time. *Compsemys plicatulus* was found to be a very abundant form in this horizon and it was possible to study nearly all the parts of the skeleton. Of the Laramie forms nothing but the shell is known so far, and this shows all the characters of the Jurassic form; it is therefore impossible, at present, to separate the Laramie and Jurassic tortoises generically from each other. The Laramie form very often has all the elements of the carapace and plastron so strongly united, that the sutures, especially on the plastron, cannot be distinguished. In a short note on the classification of the Testudinata,[7] I have given the principal characters of the generalized sub-order Amphichelydia, Lydekker. These characters were gained from the study of the Jurassic form *Compsemys plicatulus* Cope. They are: "Nasals free; a squamoso-parietal arch; descending processes of prefrontals joining vomer; stapes in an open groove of the quadrate; pterygoids narrow in the middle, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid well developed and free; dentary bones distinct. Cervical vertebræ with well developed transverse processes, more in front of vertebra, with single articular faces, biconcave; dorsal vertebræ, sacral vertebræ, with well-developed ribs; ribs of sacral vertebræ connected with centrum and neuroid. Pelvis not anchylosed to the carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of peripheralia connected with the ribs."

[7] Baur, G. On the Classification of the Testudinata. American Naturalist, June, 1890, pp. 530–536.

Shortly after this a note appeared by Prof. Marsh[8] in the August number of the American Journal of Science, entitled: "Notice of Some Extinct Testudinata."

In this paper *Compsemys plicatulus* appears under a new generic and specific name: *Glyptops ornatus*, Marsh. The skull, as figured in Pl. VII, fig. 1, gives only an idea of the general shape. The description is given in the following words: "A striking feature of this skull is that its entire external surface is elaborately sculptured. This character, hitherto unknown in the Testudinata, has suggested the name proposed.

"In its general features, this skull resembles that of *Chelydra serpentina* Linn. It is wedge-shaped in form, when seen from above. The orbits are small, and well in front. The nasal opening is directed upward, rather than forward. The premaxillaries project downward in front into a tooth-like beak. The nasals appear to be distinct. The maxillaries are deeply grooved below, but show no indications of true teeth. The skull is roofed over posteriorly, as in *Chelone*, and some other sea-turtles.

"There is a posttemporal arch. The occipital condyle is nearly round, and has a deep pit in the center. The condyle is formed entirely of the basioccipital, as the thin exoccipital plates do not reach the articular surface. The basioccipital processes are prominent and directed backward. The pterygoids separate the quadrates and the basisphenoid. At their union with each other, they are much constricted, but expand in front. The quadrate is stout and curved, and its articular face is deeply notched.

"The lower jaws referred to this species are slender and much less sculptured than the skull. The dentary bones unite at the symphysis by a short, open suture and form a sharp, elevated point to meet the decurved tooth-like beak above. The upper border is quite sharp, and fits well into the deep alveolar sulcus of the maxillary."

The Skull.

I shall go now successively over those characters which are not quite correct. It is an interesting and important fact that the sculpturing of the skull agrees *exactly* with the sculpturing of the carapace and plastron. The nasals are distinct and meet in the

[8] Marsh, O. C. Notice of some Extinct Testudinata. Am. Journ. Sc., vol. XL, August, 1890, pp. 177–179, pl. VII, VIII.

median line; the same character I have observed in the skull of *Toxochelys* from the Cretaceous of Kansas.

Prof. Marsh says the maxillaries show no indications of true teeth; but they show no indications of teeth whatever and are not different in this respect from any other Testudinata living or extinct.

It is stated that "the skull is roofed over posteriorly, as in *Chelone* and some other sea-turtles." It is a character of *all* the sea-turtles (Pinnata) to have the skull roofed over.

"There is a post-temporal arch." I do not know what Professor Marsh wants to express by this.

"The occipital condyle is nearly round and has a deep pit in the center." This pit is very common among the Testudinata and is found always where the basioccipital meets the exoccipitals. The statement that "the condyle is formed entirely of the basioccipital" is incorrect. The exoccipitals take part in the formation of the condyle just as in *Chelydra*. If Professor Marsh means by "exoccipital plates," the upper part of the exoccipital, he is right in the statement that they do not reach the articular surface. They do not reach this surface in any of the Testudinata.

I shall now give some supplementary remarks on the same skull.

At first it must be stated that the sutures are very difficult to distinguish, and that I was unable to define them on the upper part of the skull, with the exception of the nasals and the median suture. As stated before, the whole skull is sculptured like the shell. It is somewhat compressed laterally behind, and is therefore broader than shown in Prof. Marsh's figure. Seen from the side it resembles very much the skull of *Chelydra*, but is even more emarginated in the region where the jugal meets the quadratojugal. The whole palatal aspect agrees with *Chelydra*; the foramina palatina are very large. The petrosal is not produced in front. The orbit is not closed behind by bone, but is open. The skull as a whole shows characters which we expect to find in the ancestors of Cryptodira and Pleurodira.

The quadrate resembles mostly that of the Pinnata, the whole arrangement of palate, pterygoid, basisphenoid is that of the Cryptodira, the presence of the epipterygoid is also a character of the Cryptodira and so is the union of the descending processes of the prefrontal with the vomer. But the free nasals, the suturally united dentary bones, and the absence of the production[1] of the petrosal are characteristic of the Pleurodira.

[1] This production is only absent in *Dermochelys* among the Cryptodira.

The Cryptodira developed from the Amphichelydia of which *Compsemys* is the best known member, by the union of the nasals with the prefrontals; the union of the dentary bones, and the development of the production on the petrosal. The Pleurodira developed from the Amphichelydia, by the lateral expansion of the pterygoid bones, the reduction of the posterior process of these bones, resulting in the non-separation of quadrates and basi-sphenoid, by the disappearance of the union between vomer and descending processes of prefrontals, and the disappearance of the epipterygoid as a separate element.

I have now to discuss the other parts of the skeleton.

Carapace and Plastron.

Prof. Marsh thinks that the carapace represented in Plate VII, fig. 2 was not found with the "skull, and may possibly represent a distinct form." There is not the slightest proof of the latter statement. First, as mentioned above, the skull shows exactly the same (not similar, Marsh) sculpture as the shell; and second all the numerous remains of tortoises from this locality belong to the genus *Compsemys*, and probably to the same species, *Compsemys plicatulus*, Cope.

I. *Dermal Shields or Scutes.* (*Scuta.*)*

a. Carapace.
Vertebral-scutes.
Lateral-scutes.
Supramarginal-scutes (among living Testudinata only in *Macrochelys*).

b. Disc.
Marginal-scutes, the front one generally called nuchal shield, I called *cervical*, to distinguish it from the underlying bone (nuchal-bone). The posterior one, if single, I called *caudal*-scute.

c. Plastron.
Intergulare (ia).
Gularia.
Brachialia.
Pectoralia.
Abdominalia.
Femoralia.
Analia.
Interanale (only in Cheloniidae).
Inframarginalia (Axillare, Inguinale).
Submarginalia (only seen in a great number of a young *Chelonia* spec. from the Galapagos Islands [Am. Nat., May, 1890, p. 487]).

II. *Dermal Ossifications.*

a. Carapace.
Neuralia.
Postneuralia (the elements between the last neural and the pygale).
Pleuralia (generally called costal bones).

b. Disc.
Peripheralia (generally called marginal bones), nuchale, pygale.

*I have adopted the above nomenclature for the dermal shields and dermal ossifications of the carapace and plastron of the Testudinata. (Zool. Anz., No. 285, 1888.)

c. Plastron.
Epiplastron=clavicle+dermal ossification.
Endoplastron=interclavicle+dermal ossification.
Hyoplastron, Mesoplastron, Hypoplastron, Xiphiplastron } =abdominal ribs+dermal ossification.

In the figure of the carapace given by Prof. Marsh no indication of the impressions of dermal shields is to be seen. I may state, that the shields become indistinct in old individuals, but can generally be seen on the peripherals (marginals). There is a distinct cervical (nuchal) in this genus, the vertebral shields are very broad. There are eight neuralia and two post-neuralia all touching each other and preventing the pleuralia from meeting in the middle line. In the drawing given by Prof. Marsh, which is partially restored, only one postneural is given, but in other specimens two such elements are present. Pleurale has a sharp edge on its lower side as in Pleurodira and some Cryptodira. The hyoplastron is united to the first pleural bones by gomphosis; there is a distinct groove for the union with this element; the hypoplastron reaches the pleurale 5 and 6; on the union of both a short but deep groove for the end of the hypoplastron is found. The plastron is united with the carapace by gomphosis, and reaches from pleur. 2 to pleurale 8. The ends of the ribs project a little over the end of the pleuralia.

The plastron is rounded behind, and only very little emarginated. The median end of the right mesoplastron is not so broad as that of the left one; and both the mesoplastra become attenuated at the middle. The Xiphiplastron shows a small pit for the reception of the pubis. The dermal shields agree essentially with Pleurosternon.

The Vertebræ.

1. *Cervicals.* The most remarkable fact in the cervical vertebræ is that they are bicœlous; like the Pleurodira, they have single articular faces and show no ginglymoid articulations like the Cryptodira and Trionychia. In a former paper[1] I have tabulated the different modifications found in the living Testudinata; it is very much to be regretted that so very little or hardly anything is known about the condition found in the older fossil forms. *Chitracephalus* Dollo has all the cervicals preserved, but nothing is published yet about the condition of the articular faces, which probably show some interesting points and may help to explain the arrangement

[1] Bauer, G. Revision meiner Mittheilungen im Zoologischen Anzeiger mit Nachtraegen. (Die Halswirbel der Testudinata.) Zool. Anz. No. 306, 1889.

seen in the Trionychia. The splendid specimens of *Idiochelys* in the Museum of Lyons (France), also have the cervicals preserved, but we know nothing about their structure.

In the living Testudinata we find the following conditions:—

I. Ginglymoid-articulations absent.

a. Only one vertebra biconvex, the *second;* all the following concavo-convex: *Podocnemididae,*[1] *Sternothaeridae.*

b. Two vertebræ biconvex, the *fifth* and the *eighth;* 2–4 convex-concave, 6 concave-convex, 7 biconcave: *Chelyiidae.*

II. Ginglymoid-articulations present.

a. Only one vertebra biconvex.

1. The *second,* Dermatemydidae.[2]
2. The *third,* Staurotypidae, Cinosternidae.
3. The *fourth,* Chelydridae, Cheloniidae, Dermochelyiidæ.
4. The *fifth,* one specimen of *Chelonia Mydas,* in the Natural History Mus., Brussels.
5. The *sixth;* not known.
6. The *seventh;* not known.
7. The *eighth;* not known in this group but one specimen of *Testudo Leithii* in the Peabody Mus. shows this condition.

b. Two vertebræ biconvex; one of these is always the eighth; the other may be

1. The *second,* one specimen of one of the Testudinidae, species not defined (Vaillant).
2. The *third,* Testudinidae, part, Emydidae part.
3. The *fourth,* Testudinidae, part, Emydidae part, Platysternidae.
4. The *fifth,* a single specimen of *Testudo tabulata* Walb. (Smithsonian Institution.)
5. The *sixth,* not known.
6. The *seventh;* impossible.

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[1] The saddle-shaped articular faces of some cervicals in the Podocnemididae (*Podocnemis, Peltocephalus*) described by me (Zool. Anz. No. 298, 1888 and Amer. Naturalist, May, 1890, pp. 482–484) have to be considered as derived from a form like *Erymnochelys* and the Sternothaeridae (*Sternothaerus, Pelomedusa*).

[2] This condition I have also observed in a single specimen of the Cinosternidae, *C. flavescens.*

c. All vertebræ convex-concave: *Trionychia.*[1]

d. All vertebræ concave-convex: *Pyxis.*

From this list we see, that in all living Testudinata the posterior articular face of the eighth cervical (the Trionychia perhaps excepted) is convex; the anterior face of the first dorsal, therefore, concave. In *Compsemys* the first dorsal has this face also concave; we ought to expect, therefore, that the eighth cervical has the posterior articular face convex, but this is not the case. In the vertebra which I consider the eighth the posterior articular face consists of two portions. The upper one which corresponds to the original central part is slightly concave, the lower one which extends to the median keel on the lower side of the vertebra is convex. The tendency is there to form a convex articular face, but the original concave condition is still visible. The anterior face is slightly concave. The neuroids are elevated, the postzygapophyses are horizontal, very near together but not confluent. In the seventh cervical we have similar conditions, but the articular faces are more concave than in the eighth. There are two other vertebræ which I consider as the second and third, both are biconcave, but the neuroids are not elevated. In all these vertebræ the zygapophyses are horizontal; the lower side of the vertebræ are provided with a keel; the diapophyses are well developed and are not placed entirely in the middle,[2] but more in front; there is no neurocentral suture. All these conditions agree more with the Pleurodira than with the Cryptodira. It may be possible that the vertebræ between the third and seventh may be of different condition, but this is not probable, because even the 8th

[1] It is a very remarkable fact, that in *Trionyx foveatus* Leidy, from the Laramie, of which I have worked out and studied a nearly complete specimen in the Peabody Museum, collected by J. B. Hatcher, the cervicals show exactly the same condition as in the living forms; even the posterior face of the 8th cervical is of the same nature. It is probable that this face has been convex in the more ancient types, as in all living Testudinata, or it may have been concave as in the Amphichelydia. The Trionychia are a very old type, which has undergone hardly any morphological changes since the Laramie in which formation they make their appearance. I am unable to find any generic difference in the splendid Laramie species, from the living American forms of *Trionyx*. If the skull is known it may prove to be different, but shell, vertebræ and limbs do not allow a generic separation. I may mention here the interesting fact, that the Trionychia are found to-day in rivers and also lakes in which we also find the old representatives of fishes. In North America, the Trionychia are met together with *Lepidosteus, Amia, Spatularia;* in Africa with *Polypterus* and *Calamoichthys;* in Asia with *Psephurus.* Already in the Laramie we find the Trionychia together with Ginglymodi. Another similar case we see in the geographical distribution of the Pleurodira and Dipnoi; South America, Africa, Australia; and we may perhaps yet find representatives of the Dipnoi or other ancient groups in Papua.

[2] I have seen a similar case in *Peltocephalus tracaxa* Spix.

cervical, which in all living Testudinata has the posterior face convex, shows distinct traces of concavity.

The dorsals, sacrals and caudals. There are ten dorsals and two sacrals, the number of the caudals is not known.

The first dorsal is entirely pleurodiran; all the dorsals have well developed ribs which unite with the pleurals; the rib-heads are well developed. The tenth dorsal also has a rib, which broadens distally and is suturally united to the eighth pleural which contains the rib of the ninth dorsal. The rib of the tenth dorsal is often found free from the eighth pleural, and in this case this pleural contains a deep groove for the rib. The rib of the tenth dorsal reaches only to the lower middle of the eighth pleural. On the broad distal face of the tenth rib the ilium stands, exactly as in the Emydidae and Testudinidae. The neuralia are only loosely attached to the corresponding neuroids of the dorsals. All the neuroids are suturally united to each other. The two sacrals have well-developed ribs which are connected with both the centrum and the neuroids. In the first sacral the anterior and posterior neurapophyses are well developed, allowing not only a motion between the sacrum and the last dorsal, but also some motion between the two sacrals; the same we find in the Chelydridae. The first sacral is flat behind. I do not know the condition of the caudals.

From this description it results that the arrangement of the posterior dorsals and sacrals is entirely Cryptodiran and not Pleurodiran. To understand this more fully I give a synopsis of the different condition of the posterior dorsals and the sacrals in the Cryptodira, Pleurodira and Trionychia.

I. CRYPTODIRA.

1. CHELONIIDAE; ribs of tenth dorsal well developed; either (distally) suturally united with the eighth pleural (*Chelonia*) or free (*Thalassochelys*).

DERMOCHELYIDAE ribs of tenth dorsal developed; free.

CHELYDRIDAE; ribs of tenth dorsal generally absent.[1]

[1] In one case I have seen a rib on one side, in another case the ribs were present on both sides but only distally ossified. In the latter case a distinct sutural union took place with the eighth pleural and the ribs even reached the eleventh peripheral, forming a little groove there for union. In the same specimen, 676 of the Peabody Museum, the pygal was divided by a median suture. This case is interesting. Rütimeyer states that in *Platychelys* a distinct face is seen on the eighth pleural for the ilium, but this face which extends over to the eleventh peripheral, is probably nothing but the face for the union of the pleuroid of the tenth dorsal.

Staurotypidae; ribs of tenth dorsal absent.[2]

Cinosternidae; ribs of tenth dorsal absent.[2]

Dermatemydidae; ribs of tenth dorsal present, free.

Platysternidae; ribs of tenth dorsal present, suturally united with eighth pleural.

Emydidae; ribs of tenth dorsal present, suturally united with eighth pleural.

Testudinidae; ribs of tenth dorsal present, suturally united with eighth pleural.

Adocidae; ribs of tenth dorsal present, suturally united with eighth pleural.

II. PLEURODIRA.

Sternothaeridae; ribs of tenth dorsal present, suturally united with eighth pleural.

Podocnemididae; ribs of tenth dorsal present, suturally united with eighth pleural.

Chelyidae; ribs of tenth dorsal present, suturally united with eighth pleural.

III. TRIONYCHIA.

Trionychidae; ribs of tenth dorsal present, or absent, when present free.

The oldest condition seems to be a free rib on the tenth dorsal; this may become suturally united with the eighth pleural and become reduced secondarily afterwards; or it may become reduced before its union with the eighth pleural.

In the condition of the sacral vertebræ *Compsemys* agrees with the Cryptodira. I have shown in a previous communication,[3] that the sacrum of the Pleurodira has undergone great reductions, and that the sacral vertebræ have at last partially become caudals.

Nothing of this kind is to be seen in *Compsemys*, which agrees in the construction of the sacrum with the Cryptodira.

[2] In none of the Staurotypidae or Cinosternidae have I observed a rib on the tenth dorsal; in these two families, which are very close together and ought to be considered as subfamilies of a single family, to which also the Anostirinae belong, the rib-heads of the eighth pleural are always absent, so that the eighth pleural is in no connection with the tenth dorsal. This is a secondary condition, for in *Pseudotrionyx*, Dollo, which probably also belongs to this group, the rib-heads are still present.

[3] Baur, G. Osteologische Notizen über Reptilien. (Fortsetzung III.) Zool. Anz., No. 285, 1888.

We see that the vertebræ of *Compsemys* also combine characters of both the Pleurodira and Cryptodira. The Cryptodira developed by changing the condition of the cervicals; the Pleurodira by changing that of the sacrals.

The Shoulder-girdle.

The scapula and coracoid of different individuals are preserved. The scapula resembles the same element in Chelydra, but has a more slender neck. The coracoid is very much broadened distally, as in *Chelys* and some other Pleurodira and the Testudinidae. I may add here some words on the morphology of the scapula of the Testudinata. There has always been much difference of opinion about this element. The scapula consists, as is well known, of two branches. The upper one generally called scapula s. s., and the lower one, which is either regarded as precoracoid (Huxley, Parker, Gegenbaur, etc.) or as clavicle (Goette, Wiedersheim, Hoffman). That it cannot represent the clavicle is clear; because this element is contained in the epi-plastron of the plastron as I have shown definitely by the comparison of the Stegocephalia, Proganosauria and Testudinata.[1]

It remains to examine now whether it represents the precoracoid or whether it is a secondary formation of the scapula.

It is well known that we find a very similar scapula among the Plesiosauria; a step to this condition is also seen in *Metriorhynchus*, as described by Dr. Hulke in a late volume of the Proc. of the Zoological Society, which I have not at hand at present. In *Metriorhynchus* the ventral element of the scapula, which I have called proscapula,[2] is very well developed; but it is nothing but a process of the scapula. If this process becomes larger we have the conditions of the Plesiosauria and Testudinata.[3] This seems to be the only reasonable explanation. It cannot represent the precoracoid, the opinion of Huxley, Gegenbaur, Parker and others. The precoracoid, when it is free and at all recognizable, is placed between the true coracoid and the scapula outside the acetabulum, in the formation of which it may take part or not. In this condition we find it in the Monotremata and the Theromora. If the element

[1] Baur, G. Palæohatteria Credner and the Proganosauria, Am. Journ. Sc. Arts, vol. xxxvii, April, 1889. p. 312.

[2] In Zittel, Handbuch der Palaeontologie, Vol. III, p. 509.

[3] In the oldest Plesiosauria, *Nothosaurus*, *Lariosaurus*, the lower part of the scapula is also very little developed.

called precoracoid by Huxley and the others would represent really this bone, it would have a position entirely different; it would not be placed between the coracoid and scapula outside the acetabulum, but inside of it. The ventral process of the scapula in Testudinata and Plesiosauria, which I have named proscapula, seems to be, therefore, nothing but a secondary evolution.

The Pelvis.

All the elements of the pelvis are preserved in different individuals. The ilium resembles very much that in *Baëna arenosa* Leidy. It has the same posterior process as this form.

The pubis has a very massive pectineal process which stands on the xiphiplastron, the true pubis is a slender element meeting that of the other side in the middle line. The ischium is *larger* than the pubis, so that at first sight the two bones are easily confounded. The posterior process of the ischium is greatly developed and on the union of this process with the true ischium this element rests on the xiphiplastron. The branches of the ischium meet in the median line but are not united with the pubis. In structure the pelvis of *Compsemys* is between that of *Chelydra* and *Chelys*. The ancestors of *Chelys*, which had the pelvis free from carapace and plastron, must have been very much like *Compsemys* in this regard.

The Fore Limbs.

The fore limbs are long and resemble the elements of the Emydidae. The humerus is not so much curved as in the Pleurodira and resembles in shape that bone in *Terrapene;* an ectepicondylar foramen is present. The hand must have been very much like that of the Emydidae.

The hind limbs were of the same character, so far as known; the femur agreeing with the Emydidae; whether four or five claws were present cannot be stated at present.

Conclusions. From the foregoing descriptions we see that *Compsemys* is wonderfully mixed in its characters. It is half Pleurodiran half Cryptodiran. The group Amphichelydia to which it belongs must be considered as ancestral to both Cryptodira and Pleurodira. The Cryptodira developed through modification of the cervicals and the plastron; the mesoplastron disappeared successively, and in some forms also the intergular and inframarginals. The Pinnata still contain these elements, but there is no trace of a mesoplastron left.

The Dermatemydidae retain the inframarginals which become very much reduced in the Chelydridae, Staurotypidae and Cinosternidae; but none of these forms have preserved a mesoplastron. The extinct Adocidae, which belong to the same group, have lost the mesoplastron as early as in the Cretaceous, but the Jurassic *Platychelis*, which is probably an ancestor of these forms, still contains a vestige of this element. Another branch is represented by the Platysternidae, Emydidae and Testudinidae.

The Pleurodira developed from the Amphichelydia, through specialization of the head and the carapace and plastron. One of the living forms retained the complete mesoplastron (*Sternothaerus*); in others it became reduced, *Pelomedusa*, *Podocnemididae;* in others, Chelyiidae, it disappeared entirely. The inframarginals must have been reduced very early, for in none of the living forms do we find these elements; the intergular is always retained. A true Pleurodiran is present already in the Cretaceous of New Jersey, *Taphrosphys* Cope, which is identical, with very little doubt, with *Bothremys* Leidy.

The early history of the Testudinata remains as dark as before, even the oldest form we know, *Proganochelys*, which may be identical perhaps with *Chelytherium* of H. v. Meyer, gives no clue. It is a typical tortoise. It may have been, in its skull and cervicals, like *Compsemys*, but we have to wait for new material for the solution of this question. A very peculiar circumstance in the Testudinata is the small number of presacral vertebræ. The original number is eighteen; eight cervicals, ten dorsals. There is only one reptile with this number, all others have higher numbers; this reptile is the Triassic (?) *Pareiosaurus* Owen, from South Africa. Here we have also 18 presacral vertebræ. It may be that the Pareiosauria, which are a highly developed group, and the Testudinata have a common ancestor, but such ideas are nothing but speculations, which may fall at any time after a new discovery has been made. Whether we may find some day true tortoises with teeth, or whether the ancestors of the tortoises had already lost these elements, is another question, which cannot be answered to-day. The oldest skull of any tortoise we know to-day shows no indication whatever of teeth. Something which looks like an indication of the former existence of teeth is seen in *Bothremys* of Leidy, of which I have examined the type. In this form we have deep grooves in the upper and lower jaw which look very much like roots of alveoles of a large tusk;

they are very much deeper than is represented in the figure given by Prof. Leidy. This genus belongs to a peculiar family of the Pleurodira with the following characters:

Bothremydidae; *Vomer well developed; no free nasal bones, dentaries co-ossified, small mesoplastron present (in Taphrosphys, fide Cope).*

This family shows characters of the Podocnemididae and Chelyidae; like the true Pleurodira it has no descending processes of the prefrontals meeting the vomer, notwithstanding this element is present. It has no free epipterygoid and there is no production of the petrosal. In the lower jaw only the dentary bones which are firmly co-ossified, and the coronoid, which takes part in the formation of the large "alveole," just as the palate takes part in the upper jaw, are free; all the other bones are united without trace of suture, a condition present in the Podocnemididae. From such a condition to one in which the lower jaw consists only of one bony complex on each side, as seen in the Mammalia and probably the Theromora, is only a small step.

The affinities of Compsemys.

As already stated by Prof. Marsh on my authority, *Compsemys* resembles *Helochelys* from the Cretaceous Greensand, and *Pleurosternum* from the Purbeck. Of both I have examined the types in the British and Munich Museums.

Pleurosternum has the xiphiplastrals deeply notched; in *Compsemys* and *Helochelys* the plastron is rounded behind.

Pleurosternum has no nuchal shield (cervicale), in *Compsemys* and *Helochelys* this element is present.

Pleurosternum has the mesoplastron not attenuated in the middle, as in *Compsemys*, and the union of the two elements is different from that in *Compsemys*.

Helochelys has the impressions of the dermal shields very well marked, in *Compsemys* they are not distinct.[1]

The future may show that these three forms are all members of the same genus to which the name *Pleurosternum*, being the oldest, would have to be applied; but at present I think it better to accept the three genera, placing them in one family, the Pleurosternidae, as defined by Mr. R. Lydekker.[2]

[1] The shoulder girdle and pelvis seem to be very much alike in *Compsemys* and *Pleurosternum*.

[2] Lydekker, R., Catalogue of the Fossil Reptilia and Amphibia in the British Museum. Part III, p. 205; also Quart. Journ. Geol. Soc., 1889, p. 518, has described these parts in *Pleurosternum*.

Compsemys is very nearly related to the Tertiary genus *Baëna*, which has probably to be considered as its direct successor.

2. BAENA.

This genus of which *Baëna arenosa* Leidy is the type was established by Leidy in 1870. (Proc. Acad. Nat. Sci. Phila., p. 123; 1871; p. 228.) It is fully described and figured by Leidy in his Contributions to the Extinct Vertebrate Fauna of the Western Territories, Washington, 1873, pp. 160–169. Pl. XIII, figs. 1–3, XV, figs. 1–5, Pl. XVI, figs. 8–9. According to Leidy "It partook of characters of the snappers or Chelydroids, the terrapins or Emydoids, and the sea-turtles or Chelonoids." The principal characters given by Leidy are, the "two pairs of gular scute areas, which together with the other scute areas, made seven pairs to the plaston;" the presence of inframarginal scutes; and the obliteration of the sutures in the shell. To this character Prof. Cope[1] added the presence of a mesoplastron, and referred Leidy's *Chisternon*, so far characterized by the presence of this bone, to *Baëna*. He also stated, that in three species he observed five costal scuta instead of four. "The accessory one is anterior, and is taken from the usual first costal and first vertebral, both of which are contracted in consequence." Prof. Cope remarks, that "this character is unique in the order Testudinata," but it is to be found in *Lepidochelys*, (*Colpochelys*), *Thalassochelys*, and *Eurysternum*. He also states that the double intergular exists in *Tropidemys* of Rütimeyer. This is not correct; it is found in *Plesiochelys*. The presence of fourteen marginal scuta is probably coincident with the increase of the costal scuta; we find the same in *Lepidochelys* and *Thalassochelys*. In regard to the affinities Prof. Cope says: "The affinities of this genus are complex and interesting. It would be a Pleurodire, but for the fact that the pelvis is not co-ossified with the plastron; nevertheless, there are rudiments of this union in the form of a shallow pit on each side." *Baëna* is placed in a special family "Baënidae," with the characters:—Plastron uniting with the costal bones of the carapace by suture, with ascending axillary and inguinal buttresses; inter-sternal bones [mesoplastra] present; intergular scuta; caudal vertebræ opisthocœlous.

This family is adopted by Boulenger (Encyclopædia Brit., 9th ed., vol. 23, 1888, p. 457) with the following definition: "Plastral bones eleven, mesoplastra being present. Nuchal bone without

[1] Cope E. D. The Vertebrata of the Tertiary Formations of the West, Book I, Washington, 1884, pp. 144–146.

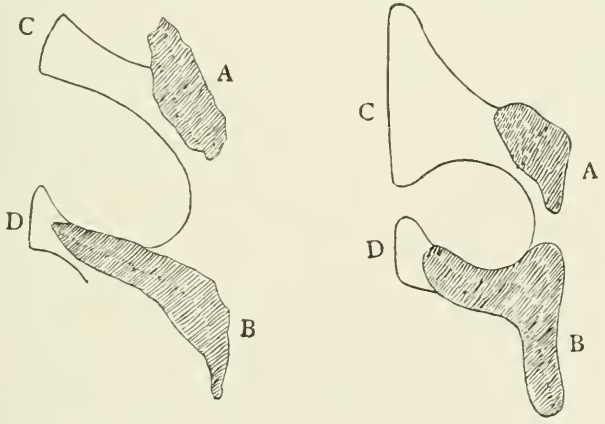
costiform processes. Carapace with epidermic scutes. Caudal vertebræ opisthocœlous."

I have studied, through the kindness of Dr. Brown Goode and Mr. Fred. A. Lucas, the type specimen of *Baëna arenosa* Leidy, now in the Smithsonian Institution. Different parts, which were still in the rock, were worked out more fully and some new points could be made out. *Baëna* proved to be nearly related to the older Laramie *Compsemys*, of which it seems to be the direct successor. The mesoplastra are more reduced, only meeting in a point in the middle line. The sutures in the carapace and plastron disappear in old specimens as in the older Laramie forms; this of course cannot be considered as a generic character, as we find the same in *Terrapene Carolina* L. in old specimens. The plastron is thickened across the axillary and inguinal region, agreeing thus with the Laramie and Jurassic *Compsemys*. The carapace is emarginated behind as described by Leidy and Cope. The dorsal vertebræ are co-ossified with each other. There are eight pleuralia very much as in *Chelydra;* the rib-heads, however, are not so long as in this genus. The third dorsal forms a sharp keel below, which also extends to the second and fourth. The tenth dorsal has a distinct rib, which is suturally united distally with the eighth pleural. The posterior face of this vertebra is deeply concave, and the center is entirely circular. The hypoplastron extends far inside between the fifth and sixth pleurals, very much as in *Chelys;* and it is probable that *Baëna* was a good swimmer. The sternal chambers are very much more developed than in *Compsemys*. The first sacral is very little convex in front, flat behind with a trifling indication of concavity. The second sacral is flat in front, concave behind. The first and second sacrals have well developed zygapophyses; the sacral ribs are united to both centrum and neuroid.

I am glad to be able to correct a gross blunder which I made some time ago. In my paper on the systematic position of *Meiolania* Owen (Ann. Mag. Nat. Hist., Jan., 1889, p. 58), I made the following remark: "All Testudinata have the second sacral vertebra convex behind. There is no exception whatever. Prof. Leidy, it is true, states that 'the posterior articular surface of the second (sacral) centrum is concave' in *Baëna*. But this is not correct: what Prof. Leidy describes as the posterior articular surface of the second, is the anterior of the first sacral vertebra. The second sacral vertebra of *Baëna* is convex behind, as in all other Testudinata."

To this idea, which is entirely wrong, I was brought by the figure given by Prof. Leidy, not by examination of the specimen. Now, after an examination of the original, I find that Prof. Leidy is absolutely correct in his statements; *the posterior articular face of the second sacral is really concave*, and the caudal vertebræ, therefore, have probably all been convex-concave or opisthocœlian. If no bicœlian vertebra appeared, it is probable that in *Compsemys*, which is not known yet in this regard, we will find the same condition.

The pelvis is directly referable to that of *Compsemys*, but is a step in advance towards the Pleurodiran type of structure. The pectineal process is short but massive, directed downwards where it meets the xiphiplastron. The inner branch of the pubis (the true pubis) is broader than in *Compsemys*. The ischium shows distally a curved rough face, which touches the xiphiplastron; there is only a step to sutural union. The ilium is figured by Leidy. The sacral ribs are touching the upper anterior part of the ilium; they are suturally united to each other at this end, the first sacral rib forming the principal portion for the attachment with the ilium. There is a small tubercle on the outer and anterior side of the ilium similar to that seen in the Cinosternidae, but very much smaller.



The sketch gives the ends of pubis and ischium meeting the plastron in *Chelys* and *Baëna*. In *Chelys* the impression of pubis and ischium on the xiphiplastron are separated considerably from each other. In *Baëna* there is a special process extending forward, with the tendency to join the impression of the pectineal process of the pubis.

Nothing is known about the skull and cervicals of *Baëna*. So far I think it best to leave *Baëna* in a special family Baënidae, nearly related to the Pleurosternidae, as proposed by Mr. Lydekker.[1] I believe that the Baënidae belong to a distinct branch of this family, which died out without leaving any successors. It is probable that the Chelydridae developed from forms similar to *Platychelys;* in which the mesoplastron was reduced more and more, until it disappeared: and in which the union between carapace and plastron became looser, until it became ligamentary. That all forms of Tortoise in which the carapace and plastron are united by ligament (*Trionychia* included) are derived from forms which had these parts united by suture, there can be no longer any doubt.

3. ADOCUS Cope.

The genus *Adocus* was established by Prof. Cope in 1868, Proc. Ac. Nat. Sci. Phila., with *Emys beatus* Leidy from the Cretaceous Greensand as type. The character was (Synopsis Batr. and Rept., p. 232). "Anterior and posterior lobe of the plastron abbreviated, narrowed, and not emarginate. Eight paired sternal bones; twelve sternal scuta, the humerals extending anteriorly, the pectorals and gulars both small. A series of plates, "intermarginals, within the marginals, in the sternal bridge. Rib-heads, *i. e.*, the capitula, wanting in the species whose costals have been examined."

To this genus is also referred Leidy's genus *Baptemys* (Synopsis, p. 233), but in the Tertiary vertebrata it appears under the name of *Dermatemys*. I have examined the type of *Adocus beatus* Leidy from the Cretaceous of New Jersey, and can say that it agrees entirely with the specimens figured by Prof. Marsh (l. c.) under the new name *Adocus punctatus*.

The specimen figured by Prof. Marsh was put together by me; it is an absolutely complete shell, both carapace and plastron in splendid condition, and I am very sorry that the latter has not been figured by Prof. Marsh. I give now the characters of *Adocus:* anterior (especially) and posterior ribs of plastron abbreviated, a little narrowed, not emarginate. Eight paired plastrals, twelve sternal shields. Inframarginals as in Pleurodira, not reaching median suture; but intergular divided by a median line. Carapace not emarginate in front, seven neural bones; the seventh separated from the sixth by the intervening seventh and eighth pleurals; one post-neural. Vertebral shields 2–5, longer than wide; costals 2–4, broader than

[1] Lydekker R. Cat. Foss. Rept. Brit. Mus., Part III, London, 1889, p. 205.

long; costals 1, extending over the peripherals; costals 2–4, placed entirely on the pleurals, cervical shield very small. Rib-heads of pleuralia very short, resembling somewhat those in the Cinosternidae. Dorsal 10, with a well-developed rib which is sutturally united distally with the eighth pleural; pelvis free from carapace and plastron.[1]

Baptemys Leidy is a distinct genus related to *Adocus;* it differs by the presence of a complete series of neural bones from both *Dermatemys* and *Adocus;* from *Adocus* it differs besides in the entirely different arrangement of the costal shields. The nuchal has a lateral process, the hyoplastron stands between periph. 2 and 3 and is only very little connected with the first pleural. It may be characterized in this way:—

Anterior and posterior lobe of plastron abbreviated and much narrower, not emarginate. Eight paired plastrals, probably twelve sternal shields; inframarginals. Carapace not emarginate in front. A complete series of neural bones. All costal shields extending over peripheral bones.

Agomphus Cope (*Amphiemys* Cope)[2] belongs also to this group and is near *Adocus.* It contains the stoutest tortoises known; the bones of the plastron of a specimen about a foot long may be nearly an inch thick. In all essential characters it agrees with *Adocus,* but the anterior and posterior lobes of the plastron are even more narrowed than in *Baptemys,* the cervical shield is more developed as in *Adocus,* the nuchal has costiform processes which reach to the second peripheral, piercing the first; something similar we see in *Dermatemys.* The sternal bridge is shorter than in *Adocus;* it reaches from the fourth to the eighth peripheral. In all these three forms eleven peripheralia are present.

The only living form that can be compared with these tortoises is the Central American genus *Dermatemys,*[3] which represents a

[1] I once believed that the ilium was sutturally united to the eighth pleural, but the suture was only the suture for the rib of the tenth dorsal.

[2] Cope E. D. A new species of Adocidae from the Tertiary of Georgia Pal. Bullet., 25, p. 2–4. Baur, G., Osteologische Notizen über Reptilien. Fortsetz. 4, Zool. Ang., 291, 1888.

[3] This genus is rare in museums, especially in the form of skeletons; the only complete skeleton I know of is preserved in the Zoological Museum of Basel; the Academy of Natural Sciences of Philadelphia is in possession of a skull; the Smithsonian Institution of shells of various ages; but I do not know of a single complete skeleton in this country; there is also no skeleton in the British Museum,

distinct family. But this genus shows considerable differences in the plastron. It is much emarginate behind, and the arrangement of the dermal shields is also different. I follow, therefore, Prof. Cope in adopting his family name Adocidae for this group.

This family may be characterized thus: *Adocidae;* Anterior and posterior lobes of plastron more or less attenuated and shortened, never emarginate behind. Twelve pairs of plastral scutes; inframarginals; no mesoplastron; neural bones complete or interrupted behind. Pelvis free from carapace and plastron.

as far as I know. This genus is very common in some parts of Central America, especially Guatemala; but all my numerous efforts to get specimens from there have been so far without success. A similar rare Central American genus is *Staurotypus*, of which I know complete skeletons only from Stuttgart, Basel and the British Museum at London.